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The Cognitive Architecture of Spatial Navigation: Hippocampal and Striatal Contributions

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Spatial navigation can serve as a model system in cognitive neuroscience, in which specific neural representations, learning rules, and control strategies can be inferred from the vast experimental literature that exists across many species, including humans. Here, we review this literature, focusing on the contributions of hippocampal and striatal systems, and attempt to outline a minimal cognitive architecture that is consistent with the experimental literature and that synthesizes previous related computational modeling. The resulting architecture includes striatal reinforcement learning based on egocentric representations of sensory states and actions, incidental Hebbian association of sensory information with allocentric state representations in the hippocampus, and arbitration of the outputs of both systems based on confidence/uncertainty in medial prefrontal cortex. We discuss the relationship between this architecture and learning in model-free and model-based systems, episodic memory, imagery, and planning, including some open questions and directions for further experiments.

Introduction

Goal-directed spatial navigation is a good model for general issues in cognitive neuroscience. Like many daily tasks, goal-directed navigation is a complex task that involves a variety of sensory and proprioceptive stimuli, storage and recall of information, and the elaboration of plans. Moreover, there is now an unparalleled literature concerning the neural representations involved (as reflected in the 2014 Nobel Prize, see e.g., Burgess, 2014) and a vast array of experimental data relating behavior to environmental or neurophysiological manipulations.

There are many ways to find a goal location, and the relevant cognitive functions have been categorized in various ways. Here, we follow the nomenclature coming from behavioral and lesion experiments in animals, following from the suggestion that the hippocampus provides a "cognitive map" (O'Keefe and Nadel, 1978; see below). Thus, one might navigate by following a sensory cue that directly indicates the goal location ("piloting"), by following a well-learned sequence of actions, each depending on the previous action or a sensory cue ("response learning" using "route" or "taxon" strategies), or by following a flexible internal representation of spatial layout ("place learning," using a "cognitive map" or "locale" strategies). The emphasis on the "flexibility" of a cognitive map refers to the ability to use it from a new starting location (which would undermine the use of a route) or in the absence of subsets of specific sensory cues (which could undermine the use of piloting or route strategies). The hypothesis that the hippocampus supports a flexible representation of the spatial relationships present in the environment has been extended to include non-spatial information in the relational theory of memory function (Cohen and Eichenbaum, 1993), in addition to its association with episodic memory rather than stimulus-response learning (Hirsh, 1974; O'Keefe and Nadel, 1978).

Here we examine the cognitive architecture of spatial navigation, with a focus on hippocampal and striatal systems and their interaction. We aim to outline the general principles that can be derived from experimental data and how they constrain the development of formal models of spatial cognition (see also Box 1).

Brain Regions Associated with Spatial Navigation

Like any complex task, spatial navigation involves much of the brain, not least sensory and motor areas. Here we review some of the systems associated with specific roles in navigation.

The hippocampus has long been known to be important for episodic memory (Scoville and Milner, 2000), and the discovery of place cells drew attention to its role in spatial memory (O'Keefe and Nadel, 1978; see below). Subsequent experiments using the Morris water maze (Morris et al., 1982), T maze alternation (e.g., Cohen et al., 1971), and the eight arm maze (e.g., Olton et al., 1977) demonstrated certain aspects of navigation to be particularly sensitive to hippocampal damage. These include navigation to an unmarked location from variable start locations and navigation that requires memory (and potentially avoidance) of previously visited locations. Equally importantly, control conditions in these tasks showed insensitivity to hippocampal damage when piloting or response learning was possible and emphasized the importance of distal cues in orienting the animal within its environment.

By contrast with the hippocampal formation, cortico-basal ganglia circuits (loops) are thought to support stimulus-response associations and procedural memories (which may underlie route learning or piloting). For example, learning of probabilistic rules can be spared in hippocampus-related amnesia but impaired in conditions affecting the striatum, such as Huntington's or Parkinson's disease (Knowlton et al., 1996). These loops connect specific neocortical areas unidirectionally to striatal subregions, which project to downstream structures such as the pallidum and the substantia nigra (SN). These areas connect

Box 1. Current Status of the Field

- Multiple spatial representations have been identified in neuronal firing and in behavior.
- There is a good mapping between representations and brain systems.
- These systems appear to combine constructively to support spatial memory in a stable environment, which implies that they can be selected between in an appropriate manner, e.g., according to a measure of "confidence" in each system (e.g., slope of value function).
- Different systems appear to use different learning rules, potentially reflecting optimization for different aspects of the task (one-shot learning for hippocampal episodic memory, prediction error for striatal action learning).

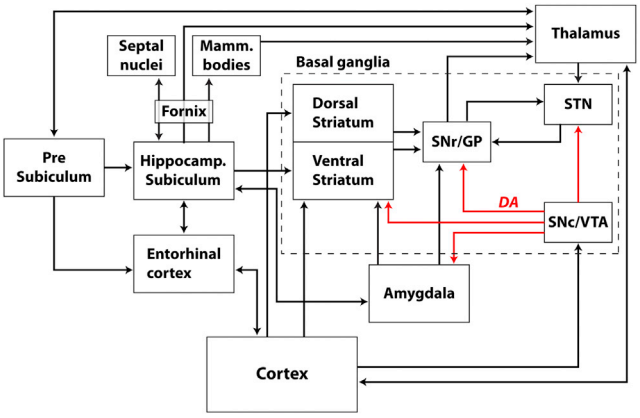

Figure 1. Simplified Schematic of the Cortical and Subcortical Connections of the Hippocampus and the Striatum

Most of the hippocampus's neocortical inputs come from the perirhinal and parahippocampal cortices (data not shown), via the entorhinal cortex. The striatum is part of the basal ganglia (including SNr, GP, SNc, and VTA), which we have here represented in a compact form for the sake of clarity. The "dorsal striatum" usually includes the caudate and putamen with the nucleus accumbens in the "ventral striatum." Abbreviations: SNr/SNc, substantia nigra pars reticulata/compacta; GP, globus pallidus; STN, sub thalamic nucleus; VTA, ventral tegmental area.

to the thalamic nuclei that in turn project back to the same neocortical sites of origin. Within this picture, the striatum has been subdivided into several functional regions: the dorsolateral striatum (DLS) associated with stimulus-response learning and habit formation, the dorsomedial striatum (DMS) associated with action-outcome learning, and ventral striatum (VS) associated with motivational and affective processing (Packard and McGaugh, 1992; Pennartz et al., 2011; Yin and Knowlton, 2006).

An important aspect of theorizing about the function of the striatum concerns its dopaminergic input. In a series of influential experiments, Schultz and colleagues recorded the firing of dopamine neurons in the SN/VTA of monkeys performing conditioning experiments. The firing of these neurons was found to be consistent with dopaminergic signaling of the reward prediction error (Schultz et al., 1997) used in theoretical models of reinforcement learning (RL; Maia, 2009; Sutton and Barto, 1981). The strong dopaminergic projections to the striatum strengthen its association with RL, with suggestions that an actor/critic-type functional architecture may map onto dorsal and ventral striatum respectively (e.g., O'Doherty et al., 2004), albeit as a major simplification of the actual functional and structural complexity of the striatum (Bornstein and Daw, 2011). The VS also receives strong projections from the hippocampus, potentially mediating associations between the distinct types of representation in the two systems (Pennartz et al., 2011; van der Meer et al., 2014; see Figure 1).

In humans, the hippocampus has been specifically implicated in accurate spatial navigation, both in terms of the effects of lesions and metabolic activity during virtual navigation, although showing a greater (right) lateralization of function than in rodents (Burgess et al., 2002). Indeed, virtual reality analogs of behavioral tests in rodents show similar associations of hippocampal and striatal activity with place and response learning, respectively. Thus, the expected dissociations are seen in terms of use of extra-maze cues and environmental boundaries compared to turns and intra-maze cues (Doeller et al., 2008; Iaria et al., 2003) and between wayfinding and route following (Hartley et al., 2003). However, the idea of a "cognitive map" has been interpreted in many ways, not all of which correspond to hippocampal activity. For example, processing a bird's eye view of the environment, which could represent "survey knowledge" but is also an egocentric representation, does not correlate with hippocampal activity (Shelton and Gabrieli, 2002).

Finally, we note the importance of the parietal cortex in spatial processing. Damage to the posterior parietal cortex often results in optic ataxia—impaired visuospatial coordination of reaching and grasping, consistent with the presence there of neurons tuned to encode the location of visual attention and aspects of reaching and grasping (e.g., Hwang et al., 2014). A common consequence of unilateral damage to the parietal cortex (most often on the right side) is a clinical syndrome known as "unilateral neglect": an impairment in noticing or paying attention to objects and events in the contralateral hemifield, or the contralateral side of objects. Patients suffering from unilateral neglect can experience "representational neglect," affecting their spatial imagery and memory performance, as distinct from the more common perceptual neglect (Bisiach and Luzzatti, 1978), with neglect in imagery (rather than perception) being more strongly linked to deficits in navigation (Guariglia et al., 2005).

Neuronal Codes

Single neuron recordings from the hippocampus of freely moving rats showed the existence of "place cells" in regions CA1 and CA3: cells that fire only when the animal is within a limited region of the environment (O'Keefe and Dostrovsky, 1971). Place cell firing patterns are established very rapidly when an animal enters an environment for the first time and are stable over the course of several days (Thompson and Best, 1990), although a slow divergence of firing patterns in the same or similar environments is seen in CA1 (Lever et al., 2002; Mankin et al., 2012; Ziv et al., 2013). This "remapping" can also reflect changes in task requirements (Markus et al., 1995) or goal locations (Dupret et al., 2010). Place cell firing patterns "remap" rapidly between distinct environments (Muller and Kubie, 1987) but are robust

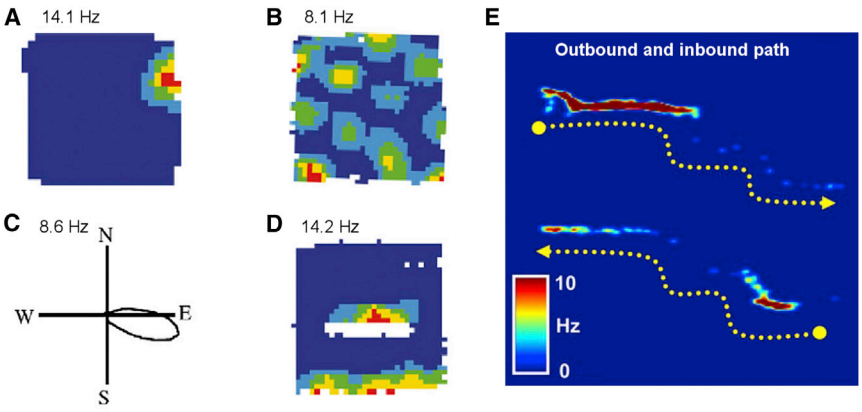

Figure 2. Examples of Spatial Cells Associated with Navigation, Recorded in Freely Moving Rats, Showing Firing Rate as a Function of Location or Head Direction

(A) Place cells, found in areas CA3 and CA1 of the hippocampus proper, typically fire in a restricted portion of the environment.

(B) Grid cells, found in medial entorhinal cortex and pre- and parasubiculum, typically fire in a regular triangular array of locations. Directional grid cells or "conjunctive" cells, whose grid-like spatial firing is also modulated by head direction, are also found in these regions.

(C) Head-direction cells, found in the presubiculum and deep layers of medial entorhinal cortex, typically fire for a narrow range of allocentric heading directions.

(D) Boundary cells, found in subiculum and entorhinal cortex, typically fire at a specific distance from an environmental boundary along a specific allocentric direction.

(E) A trajectory neuron from parietal cortex, shown for outbound (upper plots) and inbound (lower plots) traversals of a path (dashed yellow lines). Peak firing rate shown in Hz. (A)–(D) are dapted from Hartley et al. (2014); (E) is adapted from Nitz (2006), with permission.

to smaller changes such as eliminating a subset of environmental cues (O'Keefe and Conway, 1978; Quirk et al., 1990), indicating a capacity for "pattern completion" (Marr, 1971) that is associated with synaptic plasticity in CA3 (Nakazawa et al., 2002). Non-visual cues, like olfactory traces or auditory signals, can also contribute to self-location and are sufficient to guide behavior if visual cues are not accessible (Maaswinkel and Whishaw, 1999; Wallace et al., 2002). In addition, self-motion-related information is an important input to place cell firing (see below), and firing patterns also develop trajectory dependence when specific trajectories are taken repeatedly in constrained environments (McNaughton et al., 1983; Wood et al., 2000). Place cells have subsequently been identified in a wide range of mammals including bats and humans (Ekstrom et al., 2003; Ulanovsky and Moss, 2007).

A complementary representation is provided by "head direction cells." These neurons signal the orientation of the animal's head in the horizontal plane and are tuned to a narrow range of head directions centered on a preferred firing direction (Taube et al., 1990). These cells were first reported in the dorsal presubiculum (Ranck, 1985; Taube et al., 1990) and later in a network of structures along the classic Papez circuit, including the thalamic nuclei (Mizumori and Williams, 1993; Taube, 1995), mammillary bodies (Stackman and Taube, 1998), and entorhinal cortex (Sargolini et al., 2006). Interestingly, if two cells share a preferred firing direction in one environment, they will continue to respond in the same way in a second environment even if the absolute firing direction of both cells may have changed (i.e., they remain "in register"). The retrosplenial cortex provides an important input to head direction cells and seems specifically involved in associating representations of orientation to fixed elements of the external world (Clark et al., 2012; Knight and Hayman, 2014). Head direction cells have been found in other mammals, and results consistent with similar directional representations have been seen in human retrosplenial and medial parietal areas using fMRI (Baumann and Mattingley, 2012; Doeller et al., 2010; Marchette et al., 2014), including activity correlating with allocentric navigation (Wolbers and Büchel, 2005).

A third type of spatial cell, "grid cells," is found in the medial entorhinal cortex (mEC; Hafting et al., 2005) and subicular complex (Boccara et al., 2010). They share some similarities with place cells but have multiple firing fields arranged on an equilateral triangular grid that covers the environment (Figure 2B). Grid cells appear to be grouped into functional clusters within mEC that share similar characteristics: neighboring cells possess the same grid orientation and scale, having only a different translational offset, while the grid scale increases ventrally along the mEC in discrete steps (Barry et al., 2007; Stensola et al., 2012). Moreover, similarly to head direction cells, their relative position is maintained even after environmental manipulations that change or disrupt the fields of individual cells (Stensola et al., 2012; Yoon et al., 2013). Again, these cells have been found in a variety of mammals, including humans (Jacob et al., 2014), and fMRI evidence suggests that they occur throughout the autobiographical memory network (Doeller et al., 2010).

An important difference between grid cells and place cells is that grid cell firing patterns contain non-local information and so could provide a metric for large-scale navigation. Specifically, the grid cell representations of two distant locations could allow calculation of the translation vector between them (Bush et al., 2015). By contrast, place cell representations of two locations separated by more than the two place field widths contain no such information (although place fields 10 m wide have been reported; Kjelstrup et al., 2008).

The sources of information that dictate these spatial responses can be divided into self-motion and environmental sensory inputs. The strong intrinsic organization of the firing patterns of head direction and grid cells, irrespective of the sensory environment, suggests a significant influence of self-motion. Accordingly, models of head direction and grid cells often rely on continuous attractor dynamics via symmetrical recurrent connectivity (Fuhs and Touretzky, 2006; McNaughton et al., 2006; Zhang, 1996). In these models, the spatial representation is updated by self-motion (a process also known as "path integration") via asymmetric interactions (Zhang, 1996), which can be achieved by cells with a conjunctive representations of space and movement, such as head direction firing modulated by

angular velocity (e.g., Skaggs et al., 1994; Stackman and Taube, 1998) or grid cells modulated by movement velocity (Sargolini et al., 2006; see Burak and Fiete, 2009; Conklin and Eliasmith, 2005 for computational models).

However, all allocentric (i.e., world-centered) spatial signals relying on self-motion (or "path integration") need resetting relative to the environment to avoid accumulating error. Correspondingly, spatial firing patterns are strongly influenced by the environment. Distant visual cues, where available, have a controlling influence on head direction and the orientation of other spatial responses (e.g., Taube et al., 1990). The boundaries of an environment also appear to play an important role in determining the firing locations of place cells. Place cell firing patterns across manipulations of environmental shape reflect conjunctions of distances and allocentric directions to environmental boundaries (Hartley et al., 2000; O'Keefe and Burgess, 1996), whereas discrete intra-maze landmarks have relatively little influence (e.g., Cressant et al., 1997). The predicted "boundary vector cells" mediating this information were subsequently found in subiculum (Barry et al., 2006; Lever et al., 2009) and mEC (Solstad et al., 2008). Environmental boundaries also affect the firing pattern (Barry et al., 2007) and orientation (Krupic et al., 2015; Stensola et al., 2015) of grid cells, consistent with a role in reducing cumulative error (Hardcastle et al., 2015). The complete system probably combines environmental and self-motion information to estimate location and orientation.

In contrast to the explicit representation of spatial information in the hippocampal formation, the function of the striatum can be interpreted as producing (value) outcome predictions. More precisely, since DLS receives input from the somatosensory and motor cortices, it may code predictions about the execution and sensing of specific movements (Voorn et al., 2004), whereas the DMS processes inputs from dlPFC, mPFC, and anterior cingulate cortex relating to more cognitive operations (Yin and Knowlton, 2006). Moreover, neural activity in the striatum is more strongly influenced by task stage (Barnes et al., 2005), being modulated by choice points, reward delivery, and stereotyped egocentric responses (Berke et al., 2009). However, these responses do not specifically encode route-trajectory information. Evidence for this type of information is found in the posterior parietal cortex (PPC) of navigating rats (McNaughton et al., 1994; Nitz, 2006). Interestingly, in a very structured environment, place cell and grid cell firing patterns become more trajectory dependent (Derdikman et al., 2009; McNaughton et al., 1983), suggesting an influence from parietal cortex combined with a strong contextual modulation (Whitlock et al., 2012). More generally, parietal neurons tend to code all phases of the action sequences used to solve or plan a task (Fogassi et al., 2005; Harvey et al., 2012).

Posterior parietal neurons in monkeys can exhibit conjunctive "gain field" responses tuned to visual (retinotopic) receptive fields but modulated by eye, head, or body position (Andersen, 1995; Snyder et al., 1998). These responses may allow determination of the location of visual objects relative to the body or in a world-referenced frame (Pouget and Sejnowski, 1997). In particular, area 7a, which contains neurons with world-referenced gain fields (Snyder et al., 1998), projects to the parahippocampal gyrus and presubiculum and so may allow translation between egocentric parietal representations and allocentric medial temporal representations (Burgess et al., 2001; Wilber et al., 2014), potentially mediated by retrosplenial cortex (Byrne et al., 2007; Dhindsa et al., 2014; Lambrey et al., 2012). The distinction between egocentric and allocentric representations is useful in outlining the cognitive architecture of navigation. However, we do not mean to imply a strict dichotomy. For example, egocentric information (e.g., tactile and motoric inputs) can influence place cell firing rates, and striatal or parietal mechanisms can direct action toward a location in the world.

Systems Neuroscience of Spatial Learning

The dependence of place cell firing on environmental boundaries rather than intra-maze landmarks is also reflected in hippocampal-dependent navigation. Pearce et al. (1998) adapted the water maze by adding a local cue at a fixed bearing from the submerged escape platform (Figure 3A). Rats learn relatively direct paths to the goal over the course of a few trials. After four trials (one session), the escape platform and the landmark are moved together to a new location. Rats with and without hippocampal lesions both are able to reach the hidden platform but present distinct performance curves. Hippocampal lesion animals quickly locate the platform on the first trial of a new session, using the intramaze landmark as a cue (i.e., following a "piloting" strategy), whereas the control animals are slower, continuing to search at the previous location in the maze (i.e., following a cognitive map strategy). On the other hand, control animals learn the new location within each session and out-perform the lesioned animals by the fourth trial of the session. Thus, the hippocampus appears to support learning of the platform location relative to the maze, rather than the landmark, which can hinder performance when the platform location is moved. Moving the maze relative to the testing room confirms that the rats are using the boundary of the maze in combination with distal cues for orientation (e.g., Hamilton et al., 2007).

The distinct styles of learning supported by hippocampal and striatal systems are further illustrated by experiments using a "plus" maze (Packard and McGaugh, 1996; after Cohen et al., 1971). Rats were trained to approach a consistently baited arm in the plus maze, starting from the stem (Figure 3B). After several days, a single probe trial was given, in which rats were placed in a start arm opposite that used in training (see Figure 3). Control rats displayed "place learning" (i.e., going to the same allocentric location in the maze) on the day 8 probe trial and "response learning" (i.e., making the same body turn) on the day 16 probe trial, indicating that with extended training there is a shift in the systems controlling behavior. Supporting this interpretation, rats with inactivation of the striatum displayed place learning on both day 8 and day 16 probe trials, whereas rats with inactivation of the dorsal hippocampus showed no preference for place or response learning on the day 8 probe trial but displayed response learning on the day 16 probe trial. Thus, it seems that response learning, i.e., association of reward with a body turn, depends on the striatum while place learning, i.e., association of reward with an environmental location, depends on the hippocampus.

These behavioral results show nice agreement with neural firing properties, but we should note that mapping between

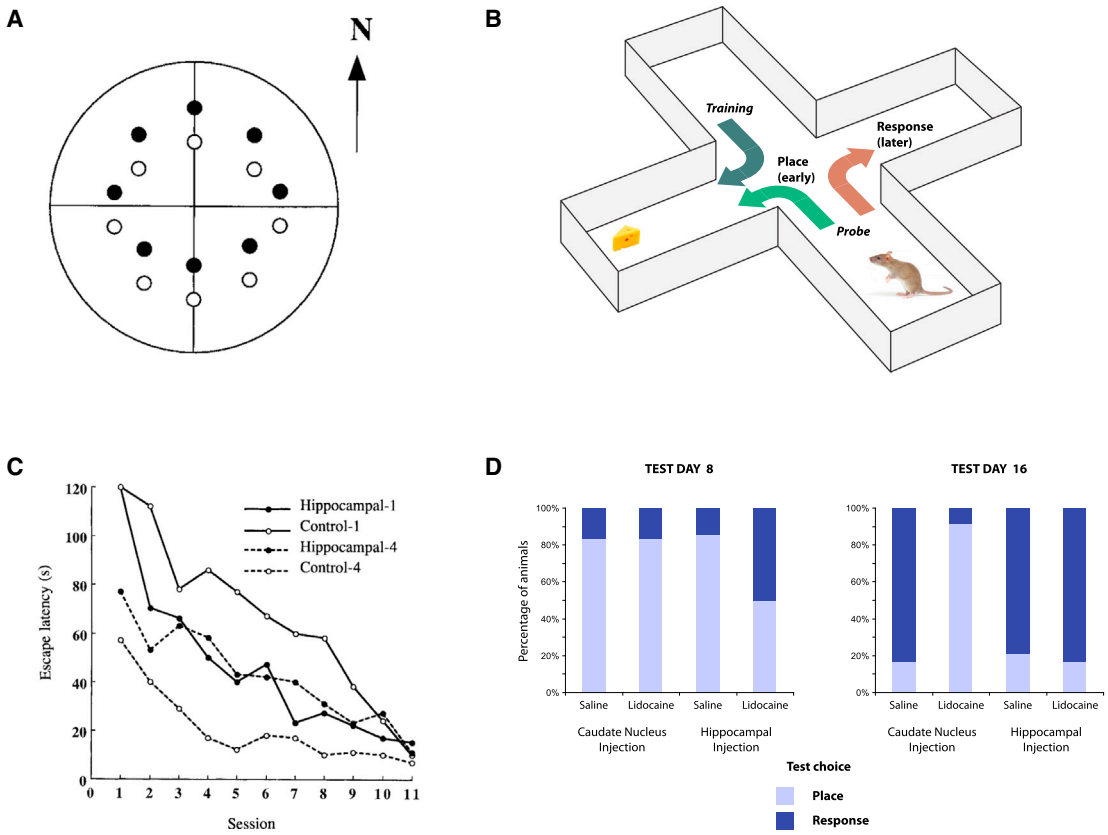

Figure 3. Examples of the Hippocampal and Striatal Contributions to Spatial Navigation

(A) Schematic of the water maze used by Pearce et al. (1998). A submerged platform (white circle) and intra-maze landmark (black circle) are placed in the maze at eight different locations on different sessions but always with a fixed offset from each other.

(B) Schematic of the plus maze used by Packard and McGaugh (1996). Rats learn to find the food placed at the end of an arm from the start location. In unrewarded probe trials, the rat's starting position is moved to the opposite side of the maze.

(C) The mean escape latency for the first (continuous line) and fourth (dashed line) trials in each of the 11 sessions for the control and hippocampal lesion rats. Adapted from Pearce et al. (1998). The hippocampal rats perform better at the start of each session, the control rats at the end of each session.

(D) Proportion of rats in the probe trials on days 8 and 16, with either lidocaine or saline injections in the caudate nucleus or hippocampus. Light bars indicate those showing a "place" strategy (i.e., going to the rewarded location in the room), while dark bars indicate those showing a "response" strategy (i.e., making the rewarded body-turn). The place strategy is sensitive to hippocampal inactivation on day 8, the response strategy to caudate inactivation on day 16. Adapted from Packard and McGaugh (1996).

neurons and behavior is not always straightforward and is complicated by the presence of multiple systems. Thus, neural responses in one system may not correspond to behaviors being controlled in part by another system. For example, an intact hippocampus may be required for the initial learning of a goal location in the corner of a box, but not when the task has been learned for many days (at which point it appears to be independent of place cell remapping (Jeffery et al., 2003). Equally, neurological patients with hippocampal damage may perform well on tests of allocentric spatial memory, especially when sufficient alternative representations could have been formed prior to the damage, for example in the striatum (see, e.g., Moscovitch et al., 2006 for discussion).

Learning Rules in Spatial Navigation

There is a long history of debate concerning the nature of spatial learning, spanning from the proponents of stimulus-response associative learning mechanisms driven by trial and error (Hull, 1943; Mackintosh, 1983; Rescorla and Wagner, 1972) to the proponents of incidental learning of internal representations capable of supporting cognition (Tolman, 1948). These arguments are brought to current thinking on spatial navigation in terms of reinforcement learning (RL) based on prediction error (Foster et al., 2000; Maia, 2009; Rescorla and Wagner, 1972; Sutton and Barto, 1981) and the proposal that the hippocampus is a "cognitive map" (O'Keefe and Nadel, 1978) or relational (Cohen and Eichenbaum, 1993) or episodic (Hirsh, 1974; Scoville and Milner, 2000) memory system.

The chief characteristic of RL is that it relies on prediction error, i.e., the difference between actual reward and expectation based on experience, as opposed to a memory system that relies on incidental one-shot association. There are several consequences of relying on a single prediction error signal. One is that only the amount of future reward associated with a choice can be used to direct behavior, but not the type of reward. To include behavior that can be "goal directed" (i.e., aimed at a specific type of reward) requires a more elaborate model of the world,

perhaps coming closer to the idea of a cognitive map. A second consequence is that learning outcomes based on multiple cues will show "blocking" and "overshadowing" (Kamin, 1969; Pavlov, 1927) between cues. Thus, if a first stimulus already fully predicts reward, learning about a second stimulus that might also predict reward will be "blocked" as there is no prediction error, and partial association of one stimulus to reward reduces the strength of association of a second concurrent cue to reward.

A recent experiment used a virtual reality adaptation of the Pearce et al. (1998) rodent experiment to test whether different types of learning occur within hippocampal and striatal systems in humans (following Hirsh, 1974; O'Keefe and Nadel, 1978). Using fMRI, this experiment showed that learning object locations relative to the environmental boundary correlated with hippocampal activity, whereas learning object locations relative to an intra-maze landmark correlated with activity in striatum (and also parietal cortex; Doeller et al., 2008; Doeller and Burgess, 2008). Moreover, parallel behavioral experiments showed that learning relative to an intra-maze landmark is blocked and overshadowed by a second cue (whether a landmark or boundary), whereas learning relative to an environmental boundaries is not—occurring incidentally to other cues (Doeller and Burgess, 2008).

Taken together, these results suggest that the striatum uses RL to associate actions to specific stimuli or landmarks that predict reward (including good performance in the case of conscientious human participants). Whereas the hippocampus forms incidental associations between objects (which might include, but is not restricted to, rewarding objects) and the environmental locations in which they are encountered. The diverse functions and learning rules of these two systems beg the question of how they interact to support a common behavioral outcome. In this context, we note that a large body of research has highlighted the role of the prefrontal cortex in the control and organization of goal-directed behavior (Tremblay and Schultz, 1999; Watanabe, 1996), the monitoring of ongoing voluntary action sequences (Gehring and Knight, 2000), the planning and selection of appropriate actions based on anticipated reward (Petrides, 1995; Rowe et al., 2000), and the ability to learn the contingency between actions and specific outcomes (Balleine and Dickinson, 1998).

The rodent medial prefrontal cortex (mPFC) comprises the ventral infralimbic cortex underneath the more dorsal prelimbic and anterior cingulate regions. The former region projects to a variety of limbic and autonomic regions, including the hypothalamus, the amygdala, and the shell region of the nucleus accumbens. In contrast, the more dorsal prelimbic region of PFC projects to core regions of the nucleus accumbens and to dorso-medial regions of the dorsal striatum, and has reciprocal indirect connections with premotor and motor cortices. Direct projections to the mPFC stem from the CA1/subiculum of the ventral part of the hippocampus (vHPC) (see Figure 1; e.g., Berendse et al., 1992; van Strien et al., 2009). Cells in mPFC can exhibit location-specific firing and lesion in vHPC disrupts goal-related activity (Burton et al., 2009). Anatomical connectivity suggests that the mPFC could be capable of integrating information from brain regions mediating (and even overriding) appetitive and emotional motivation and goal-directed and habitual responses (Smith and Graybiel, 2013; Killcross and Coutureau, 2003). Consistent with this idea, Doeller et al. (2008) found that, while activity in either hippocampus or striatum indicated use of the corresponding strategy, increased mPFC activity was seen when both systems were similarly active—suggesting a role in mediating between them.

Toward a Computational Account of Spatial Navigation

In this section, we first briefly review classical computational models of how the hippocampus and the striatum might support spatial navigation and then describe recent developments that try to reproduce the experimental and neurophysiological data reviewed above.

A number of earlier models of navigation combine the unsupervised learning of place representation with variants of RL (Brown and Sharp, 1995; Foster et al., 2000). However, this is somewhat at odds with the idea of a distinct rapid incidental learning system in the hippocampus in combination with a slower RL mechanism (see above and Lengyel and Dayan, 2007; Sheynikhovich et al., 2009) and related proposals for complementary hippocampal and neocortical learning systems (Marr, 1971, 1970; McClelland et al., 1995). Viewed as a memory system, learning in the hippocampus need not be driven by reward—its function may be to represent experience (e.g., what is encountered where, for navigation) so that it is available to future planning in which new goals may be specified. In this case, currently unrewarding stimuli may become important in the future and so also need to be remembered. Nonetheless, encoding may be biased toward stimuli that are novel, for efficiency in encoding, or toward stimuli that precede a rewarding event (see e.g., McNamara et al., 2014).

Another family of models (Blum and Abbott, 1996; Dollé et al., 2010; Martinet et al., 2011; Muller et al., 1996) utilizes the hippocampus to build graph-like representations of the environment for use in path planning using activity propagation methods. The connectivity between place cells can in principle support multiple graph-like representations (Samsonovich and McNaughton, 1997), and propagating activity is observed in place cells (e.g., Johnson and Redish, 2007; Pfeiffer and Foster, 2013). However, one issue faced by these models concerns the use of experience-dependent graph learning, which would bias behavior toward well-learned routes: an outcome more associated with the striatum.

Taking inspiration from these previous works, below we outline a minimal cognitive architecture that satisfies the functional and biological constraints reviewed above. For simplicity, we consider four main components: sensory cortex, the hippocampus, the striatum, and the prefrontal cortex (see Figure 4).

We assume that sensory cortex supports a representation of the identity and distance to objects within the view field relative to the position and direction of the head (i.e., in an egocentric frame of reference). This sensory information, or "sensory snapshot," reaches both hippocampal and striatal systems. Below we describe the different ways in which the two systems would process this information in the tasks described above (Figure 3).

As noted above, the dorsal striatum is thought to be involved in reinforcement learning of stimulus-response associations. That is, it may learn sensory motor associations using

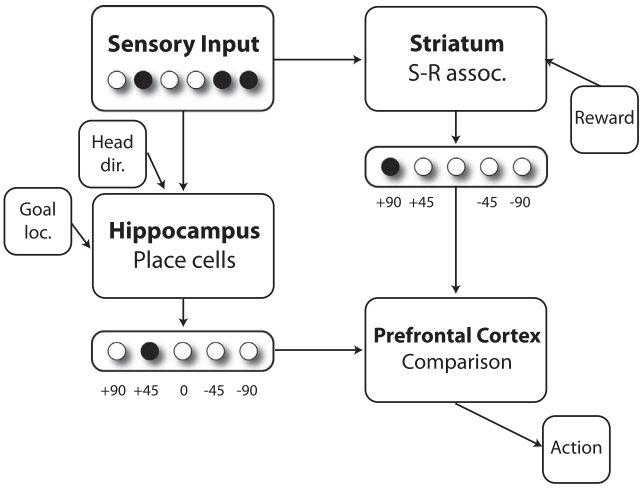

Figure 4. A Minimal Cognitive Architecture for Spatial Navigation
Schematic representation of a minimal circuit for two of the main mechanisms that guide spatial navigation: the hippocampus, providing the "cognitive map" with information about locations for goal-directed decision making, and the striatum that learns stimulus-response associations. Note that the same sensory input is used in different ways by the two systems. Basic sensory inputs reach both the striatum and the hippocampus: the former learns only when a reward signal is provided (there is no flexible goal); the latter receives additional information about the head direction and a learning signal when an important location (e.g., a goal) has been reached. Each area outputs the estimated optimal action (i.e., the turning angle), which is then compared and chosen by the prefrontal cortex.

Box 2. Future Directions

- How do the hippocampal and striatal systems influence each other during learning, and do both contribute to the calculation of a single prediction error?
- Does efficient navigation in complex environments require combinations of memory-based and reinforcement-based representations?
- What is the nature of the neural representation in the striatum and parietal cortex that support landmark-related and response learning?
- What is the exact role of "forward sweeps" of place cell activity and how do they contribute to planning?
- Are the representations of places and distances distorted by the frequency with which a route is taken, and could this problem be solved by the intrinsic regularity of grid cells?
- How is fast incidental learning implemented at a neuronal level? What determines which information is stored and which is discarded, and what role does temporal structure play?

the mismatch ("prediction error") between the outcome expected by a ventral striatal "critic" and the actual outcome in order to produce (statistically) correct associations. Thus, the dorsal and ventral striatum, respectively, have been thought of as approximating an "actor-critic" architecture for reinforcement learning (Bornstein and Daw, 2011; Pennartz et al., 2011), in which the prediction error signal is encoded by variation in dopamine (Schultz et al., 1997). Extending this line of thought, recent theories propose that different types of learning coexist within the striatum: the DLS may function as a model-free actor, while the DMS implements an additional model-based RL system. Furthermore, the ventral striatal critic may also consist of separate modules for model-based and model-free Pavlovian evaluation. In this view, the successes of dopamine-dependent learning models are preserved, and the resistance of instrumental learning to lesions of dopaminergic nuclei can be explained (Bornstein and Daw, 2011).

Given the egocentric nature of the sensory input, in which distal orientation cues are not specifically salient, the striatum will learn to associate egocentric sensory representations with egocentric actions that lead to reward (see also FitzGerald et al., 2014; Sheynikhovich et al., 2009 for discussion of how the nature of striatal state representations may be shaped by RL). In the Pearce et al. (1998) version of the water maze, for example, the most salient (reward-predictive) feature will be the intra-maze landmark due to its proximity to the submerged platform. Thus, striatal control of behavior will direct the animal to search near to the landmark. Equally, at the choice point of the plus maze used by Packard and McGaugh (1996), the egocentric sensory input will be similar from both training and probe directions. Thus, under striatal control of behavior, the sensory input associated with a specific action (body turn) during learning will also be driven by the sensory input at the choice point during probe trials.

By contrast, we suppose that the hippocampal system receives head direction information as well as sensory snapshots, so that boundary-vector cell responses can be formed to drive an allocentric place cell representation (although note that trajectory dependence might re-emerge in future models, see Box 2). Thus, the hippocampus represents states in a way that is relatively insensitive to body orientation and to discrete intra-maze landmarks compared to extended environmental features. On encountering an object of interest (e.g., a food reward or submerged platform, or a neutral object), its location can be stored by unsupervised Hebbian learning of connections from place cells to "goal cells" coding for that type of object, which might be located in subiculum, ventral striatum, or prefrontal cortex (e.g., Hok et al., 2005). The firing of these cells will then provide a value function for navigation to the object of interest—increasing with proximity to it as more of the place cells with potentiated synapses become active (Burgess and O'Keefe, 1996; see Figure 5). This mechanism, mediated by place cells, is restricted to distances of the order of the size the largest place fields (~10 m; Kjelstrup et al., 2008). Larger-scale navigation would have to rely on learned associations between place cells (see "forward sweeps," below) or on the large-scale coding properties of grid cells (Bush et al., 2015).

Although such goal cells would provide an indication of how close the animal is to the desired location, they would not indicate in which direction to move to reach it. However, the temporal characteristics of place cell firing ("theta phase precession"; O'Keefe and Recce, 1993) are such that within each cycle of the theta rhythm, the location represented by the currently active subset of place cells "sweeps forward" from behind to in front of the animal (Burgess et al., 1994; Johnson and Redish,

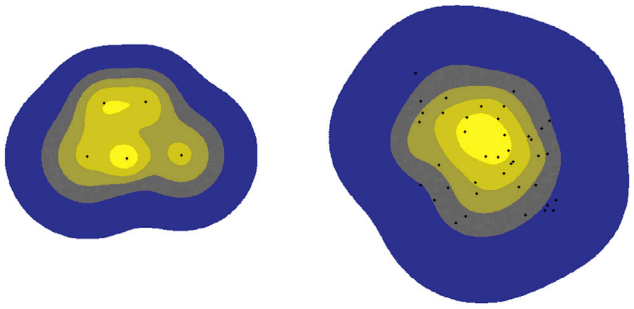

Figure 5. Schematic of How Firing Fields of Different Place Cells Can Be Combined to Obtain a Global Value Function that Can Be Used to Reach Rewarding Locations

The left panel shows an example with few neurons: when the rat reaches the rewarding site (in the center of the figures), fast Hebbian learning takes place between place cells that are active in that location (place field centers represented by black dots) and a "goal cell" downstream (e.g., in subiculum, ventral striatum, or prefrontal cortex, firing rate shown in false color). In this location, the activity of the goal cell is high (yellow colors). When the rat moves away from this location, fewer of the place cells with potentiated synapses will be active and therefore the firing rate will be lower (blue colors). The right panel shows an example with many place cells: when the number of place cells increases, the resulting value function (i.e., goal cell firing rate) becomes more regular.

2007; Skaggs et al., 1996). This potentially allows "exploration" of the suitability and the value of the current direction of travel. "Forward sweeps" and "backward sweeps" are also observed during non-locomotor behavior and sleeping (Wilson and McNaughton, 1993), with backward sweeps more prevalent after novel experience and so associated with consolidation (Diba and Buzsáki, 2007; Foster and Wilson, 2006) and forward sweeps associated with planning of upcoming trajectories (Pfeiffer and Foster, 2013). The proximity relationships between place cells, as read out by forward sweeps, implicitly encode a model of state transitions that reflects spatial structure, which may also be influenced by the presence of reward (Ólafsdóttir et al., 2015; Wikenheiser and Redish, 2013).

In order to produce a motor action or simply a decision, given the potentially different outputs from hippocampal and striatal systems, with the former having a much more cognitive character, a mechanism is necessary to compare these outputs and decide which is the most appropriate for the task at hand. One ideal candidate for this function is medial prefrontal cortex, given the fact that the comparison probably involves also the estimation of quantities such as confidence and value of information and taking into account previous decisions and outcomes (Barraclough et al., 2004). We suppose that this area selects between the possible actions indicated by either system based on the slopes of the associated value functions as a proxy for the confidence or uncertainty of the outputs of either system (Daw et al., 2005; Keramati et al., 2011). Accordingly, the time course of learning in the Packard and McGaugh (1996) experiment indicates slower striatal learning and lower confidence early on, resulting in hippocampal control of behavior, but the striatal system eventually achieves greater confidence and gains control of behavior. Similarly, in the Pearce et al. (1998) experiment, the intact animals show hippocampal control during the first trial of a new session—responding relative to the boundary of the maze, oriented by distal cues, and so performing worse than hippocampal lesion animals, due to the movement of the platform relative to the maze. On later trials within each session, however, the lesioned animals have improved little, with the intact animals now out-performing them.

Discussion

Taking inspiration from behavioral, lesion and inactivation, neuroimaging, and electrophysiological studies together with existing computational models, we sought to outline a minimal cognitive architecture for spatial navigation. Principal functional components of this architecture include the basal ganglia/striatum and the hippocampal formation, the former using local, incremental, and statistically efficient reinforcement learning rules, and the latter using a one-shot incidental learning rule. The striatal system can efficiently learn to solve key experimental tasks, such as the water maze and the plus maze, but its learning is slow and behavior is characterized by the egocentric nature of the sensory state information and the coding of actions.

By contrast, the hippocampus possesses a goal-independent representation of space that is learned rapidly, perhaps reflecting its role in episodic memory. This is obtained by having place cells initially driven in a fixed feedforward manner by their proximity relations to environmental boundaries (see e.g., Hartley et al., 2000), followed by slower adjustments as an environment becomes familiar (see e.g., Barry and Burgess, 2007; Lever et al., 2002) and the potentially related adjustment of grid cells (Barry et al., 2012). When an object or goal is encountered, "goal" cells can be formed by rapid incidental Hebbian learning in connections from place cells, so that their activity can provide gradients that can be used for goal-directed navigation (Burgess and O'Keefe, 1996; Foster et al., 2000). Behavior in this case is characterized by the allocentric nature of the representations of current and goal locations.

These two systems appear to play complementary roles at different stages of spatial learning. The hippocampus provides an initial rapid associative memory for associations between a goal (or a neutral object) and its context (environmental location in this case) that can guide goal-directed navigation in response to an explicit desire for that goal. However, the contextual association (in this case place cells) provides a similarity gradient that might not be sufficient to support navigation within complex environments. By contrast, the striatal reinforcement learning mechanism is capable of learning the statistics of the task over multiple trials, and thus potentially learning state-action trajectories that cannot be directly inferred from contextual similarity.

The outputs of these two systems must be coordinated by a third component, potentially corresponding to medial prefrontal cortex (see also Chersi and Pezzulo, 2012; Dollé et al., 2010; Sheynikhovich et al., 2009). The most obvious mechanism for selection is a comparison of the "confidence" in movement directions signaled by either system, possibly utilizing the local gradient of the normalized value function expressed by each system. This proposed architecture relates to more general models of decision making (Daw et al., 2005; Dayan, 2009), which emphasize that goal-directed and habitual mechanisms of choice are linked to model-based and model-free methods of reinforcement learning, respectively.

However, the mapping of habitual and goal-directed (as in, e.g., sensitive to devaluation of the type of reward) mechanisms onto hippocampal and striatal learning systems is not straight forward. Both mechanisms may exist outside of the hippocampus, with some authors implicating striatum in habitual learning and prefrontal cortex in goal-directed learning. In this context, the hippocampal system can be seen as a "third way" (Lengyel and Dayan, 2007): it is not just another model-based reinforcement learning system but appears to be best characterized by one-shot incidental learning of specific examples, as consistent with its well-recognized role in episodic memory (Cohen and Eichenbaum, 1993; Hirsh, 1974; O'Keefe and Nadel, 1978; Scoville and Milner, 2000).

Nonetheless, the hippocampal system can certainly play the role of the "model" in a model-based learning system. Specifically, the relationship between an explicit memory system and a means of generating imagery for planning is now being recognized. Thus, the hippocampus can be seen as the highest level in a generative model capable of consolidating memory in neocortex (Káli and Dayan, 2004, 2000). It can also be seen as a system for enabling information from long-term memory to be rendered in parietal cortex as a coherent egocentric spatial scene consistent with a single viewpoint (Burgess et al., 2001; Byrne et al., 2007). This would explain the hippocampal role in imagery for spatial layout (Hassabis and Maguire, 2007; Schacter and Addis, 2007), but not for single objects (Kim et al., 2015). In either case, the hippocampal system can be used to generate information corresponding to upcoming states for use in planning, as consistent with recent experiments showing that self-generated place cell sequences do not necessarily reproduce the animal's most frequent behavior and instead sometimes generate paths never traversed by the animal (Gupta et al., 2010; Ólafsdóttir et al., 2015).

Within the view of the hippocampus as a generative model or means of imagining future states, the imagined movement of the agent could be achieved by iterative interactions with parietal cortex (Byrne et al., 2007; Chersi et al., 2013) or by the generation of "forward sweeps" of place cell representations either during theta states (Burgess et al., 1994; Johnson and Redish, 2007; Singer et al., 2013; Skaggs et al., 1996) or offline "replay" (Pfeiffer and Foster, 2013; Wilson and McNaughton, 1993). These schemes can be seen as architectures for iterative decision making (Penny et al., 2013) and may enable the striatum to access the expected value associated with specific environmental locations (Lansink et al., 2008; van der Meer and Redish, 2009). In the context of imagery and planning, the medial prefrontal and striatal areas appear to be involved in representing the reward value of elements of imagined scenarios (Benoit et al., 2014; Lin et al., 2015).

Open Questions

The tremendous amount of knowledge about the functioning of spatial navigation mechanisms, reviewed above, gives rise to several open questions, which we discuss below, and summarize as a brief list of future directions in Box 2.

Although the hippocampus and the striatum appear to learn by two very different mechanisms, how does each system influence the other during learning? Does the information from the hippocampus directly contribute to the calculation of the prediction error in the striatal system, or is its influence only indirect via behavior (e.g., providing examples of successful routes early in learning)? Although experimental manipulations can bring the outputs of both systems into conflict, there is little evidence of direct competition between them (i.e., mutual inhibition) rather than greater activity in whichever system is controlling behavior (Doeller et al., 2008). A puzzle here is that if hippocampal information is available to the "critic," early hippocampal learning would block subsequent learning by the striatum, but if it is not, why does learning locations relative to the boundary block learning to relative to the landmark in Doeller and Burgess (2008)?

The vast amount of experimental data, both behavioral and neurophysiological, acquired in simple environments allows rather precise hypotheses on the functioning of spatial navigation mechanisms. On the contrary, information from complex mazes is less complete and less is known about planning and decision making in these environments, and how this kind of knowledge is represented in the brain. It may be that combinations of memory-based and reinforcement-based learning are employed, such as eligibility traces or saliency-based learning. Thus, it may be that the trajectory dependence of place cell firing in constrained environments (e.g., Wood et al., 2000) reflects the experience-dependent modifications of a purely spatial code to aid navigation in complex environments (e.g., Stachenfeld et al., 2014).

The striatum and parietal cortex are strongly implicated in supporting landmark-related and response learning, but our knowledge of the neural representations supporting these behaviors is still incomplete. Are similar representations present in both regions, or are there multiple such representations, and if so what are they like? The Packard and McGaugh (1996) study implies striatal encoding of an egocentric body turn, whereas the Pearce et al., (1998) study implies that hippocampal lesion animals can navigate to an allocentric vector from a landmark; however, it is possible that their sub-optimal performance reflects a failure of allocentric representation (e.g., having to circle the landmark).

"Forward sweeps" of place cell activity have been implicated in planning of future trajectories. However, the mechanisms behind these sweeps, and how they could be directed or used for "mental exploration," remain unclear. Critical questions concern the relationship between forward sweeps combined with ripples during stationary periods and those that occur as a consequence of theta phase precession during locomotion, and how both of these relate to behavioral choices during free navigation of complex environments rather than well-practiced trajectories.

One mechanism for using place cells to guide navigation (e.g., Blum and Abbott, 1996) and potentially to relating to forward sweeps is to form experience-dependent associations between place cells along frequently taken routes. However, this means that the inferred distances between places will be distorted by the frequency with which a route is taken, rather than reflecting distance per se. A potential solution for large-scale vector navigation could be to make use of the intrinsic metrical regularity of grid cell firing patterns to infer the translation vector between locations (Bush et al., 2015), but only if they are able to provide global metrical representations of complex environments, as indicated by Carpenter et al. (2015).

The hippocampus has been proposed to perform one-shot learning, consistent with its role in episodic memory, but how exactly would such a fast, incidental, learning rule work? Encounters with non-rewarding objects are encoded into episodic memory, but not all coincidences of stimuli can be encoded: what determines which are and which are not forgotten? Do they have to be followed by a significant (e.g., rewarding) event as per schema theory (Tse et al., 2007). Novelty must boost learning (e.g., one-shot learning is presumably restricted to the first experience), but how does the role of novelty in the hippocampus compare to that of reward prediction error in the striatum, and do both involve dopamine (e.g., Guitart-Masip et al., 2014)? In addition, is the temporal or ordinal structure of the task being represented in place cell firing, which could explain the temporal evolution of firing patterns in CA1 (Kraus et al., 2013; Mankin et al., 2012; Manns et al., 2007; Ziv et al., 2013), consistent with the use of temporal context in memory retrieval (e.g., Howard and Kahana, 1999)?

Conclusion

We hope to have shown that spatial navigation can serve as a model system in cognitive neuroscience, in which specific representations, learning rules, and control strategies can be inferred from the vast experimental literature that exists across many species, including humans. In this brief Perspective, we have attempted to outline a minimal cognitive architecture consistent with the most obvious of these inferences, both to demonstrate its utility as a model system and to encourage further theoretical and experimental elaboration.

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